

FACTORS AFFECTING UNDERSTORY ESTABLISHMENT IN COASTAL SAGE SCRUB RESTORATION

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ABSTRACT

Coastal sage scrub (CSS) is a target for restoration because it provides habitat for numerous special-status species and it has been impacted by urbanization, agriculture and invasion by non-native species. Many restoration designs have neglected the herbaceous understory component of CSS, although it may comprise the majority of vascular plant species in a natural CSS stand. The omission of an understory may promote invasion by non-native plants and reduce overall success. This study investigated the role of native seed addition, non-native species removal, gaps in the shrub canopy, and soil moisture, upon establishment of a native understory. Native biomass increased significantly with seed addition, and the abundance of experimentally seeded native species was positively correlated with soil moisture. Natives were not affected by competition with non-natives or the presence of gaps. Although all seeded native species germinated, only two of seven established successfully, perhaps due to very low rainfall. Non-native species were negatively affected by the addition of native seeds and had greater growth in gaps. We conclude that planting shrubs in a dense configuration to reduce gap size may reduce non-native species abundance in the understory while having little effect on the native understory. Seeding may be all that is required to establish a native understory, and may also be an effective method of suppressing non-native species.

Key Words: coastal sage scrub, restoration, competition, invasive species, seed limitation.

Coastal sage scrub (CSS) is one of the most endangered habitats in southern California. Estimates of CSS loss vary, however it is likely that CSS currently occupies less than half of its historical distribution (Westman 1981; O'Leary 1995). Primary causes of CSS loss are urbanization, agriculture, and the degradation and replacement of natural stands by the invasion of non-native species, mostly annual grasses from the Mediterranean region (Freudenberger et al. 1987; O'Leary and Westman 1988; O'Leary 1995; Minnich and Dezzani 1998). These ecosystem stressors, as well as the importance of CSS as habitat for numerous rare, threatened, or endangered plants and animals, make the community a priority for conservation (Davis et al. 1994). Regional multi species habitat conservation plans throughout southern California anticipate additional loss of CSS and require both preservation and restoration of CSS to mitigate for this loss. Thus, development is resulting in increasing numbers of CSS restoration sites, making successful restoration strategies essential for effective CSS conservation.

Typical CSS has a dense shrub canopy 0.5–1.5 m in height and a sparse herbaceous understory of primarily annual species concentrated in gaps between shrubs. Invasive non-native species are increasingly common in CSS understories (O'Leary 1995). Non-natives are undesirable in restoration projects because they reduce the success of planted shrubs (Eliaeson and Allen

1997) and compete with native understory herbs. Although many restoration designs target only the native shrub canopy, restoration of the understory as well is a more logical approach (Bowler 2000). Thus, understanding the ecological factors controlling understory structure and composition is important.

Previous studies have suggested numerous mechanisms involved in competition between non-native and native plant species. Competition with non-native annual grasses for soil moisture often limits the success of native perennials (Melgoza et al. 1990; Eliaeson and Allen 1997; Humphrey and Schupp 2004; but see Seabloom et al. 2003a). Competition with non-natives for soil moisture could also have an impact upon native understory annuals, although this has not been directly tested in CSS. Reduced light availability beneath shrubs may also reduce understory growth, resulting in a relatively higher density of understory plants in gaps, and shading from non-native grasses growing in gaps may affect these native plants (Thompson and Harper 1988; Dyer and Rice 1999).

Coastal sage scrub understories share many species with California's coastal grasslands. In two coastal grassland experiments in California, Seabloom and colleagues found that native perennial grasses (2003a) and annual forbs (2003b) were strongly seed-limited. Following seed addition, natives successfully established despite competition from non-natives. These

TABLE 1. SEEDING DENSITY, % EMERGENCE, AND RELATIVE SUCCESS OF NATIVE ANNUAL PLANTS ADDED. Biomass values (± 1 SE) were calculated from seed addition plots only. Seed emergence data were obtained from S&S Seeds (Carpinteria, CA).

Species	N seeds added/plot	% Seed Emergence	Mean end of season biomass (g m ⁻²)
<i>Amsinckia menziesii</i> (Boraginaceae)	280	54	0.38 \pm 0.15
<i>Cryptantha nuricata</i> (Boraginaceae)	990	26	0.00
<i>Lasthenia californica</i> (Asteraceae)	6240	80	8.03 \pm 2.31
<i>Lepidium nitidum</i> (Brassicaceae)	970	51	0.00
<i>Plantago erecta</i> (Plantaginaceae)	360	88	0.00
<i>Lupinus bicolor</i> (Fabaceae)	190	85	0.00
<i>Lupinus truncatus</i> (Fabaceae)	60	91	0.00

results suggest that seed limitation also could explain the failure of many restored CSS communities to develop a native understory.

This experiment's objective was to identify the primary factors limiting establishment of native understory herbs during CSS restoration. Limitation likely results from several interacting factors. Through an experimental restoration, we addressed the following four questions: 1. Is seed addition alone sufficient to restore a CSS native understory? 2. Do non-native and native understory plants compete with one another? 3. Does the reduced light environment beneath mature shrubs reduce the growth of understory plants? 4. Does soil moisture affect native understory establishment and competition with non-natives?

METHODS

Site Description

This experiment was conducted on an existing CSS restoration site adjacent to the University of California, Irvine Arboretum and UC Natural Reserve System's San Joaquin Freshwater Marsh Reserve. Prior to restoration in 2002, this site was an abandoned agricultural field that had no resident native taxa and was dominated by non-native species including *Brassica nigra* (Brassicaceae), *Foeniculum vulgare* (Apiaceae), *Cynara cardunculus* (Asteraceae), and annual grasses, primarily of the genus *Bromus*. (Nomenclature follows Hickman 1993) These same species dominated the area surrounding the site. Annual rainfall in the area is approximately 300 mm yr⁻¹.

During October–November 2002, *Artemisia californica* (Asteraceae) shrubs were planted in circular clusters approximately 3 m in diameter. Shrubs were planted at an average density of 2.5 plantings m⁻². To minimize mortality during establishment, plantings were watered weekly until February 2003, and were hand-weeded during the first spring (2003). No herbicides were applied at any time during restoration.

Experimental Design

This experiment was conducted during February–May 2004, 1.5 years after the *A. californica* clusters were planted. Native propagule abundance was manipulated by adding native seeds of five native annual forbs and two annual legumes (Table 1). Presence of non-native species was manipulated by clipping all non-native species at ground level. Seed addition and non-native removal were combined in all possible combinations, resulting in the following four plot types: 1. Native seeds added, non-native species removed; 2. Native seeds added, no removal; 3. No seed addition, non-native species removed; and 4. No seed addition and no removal.

Experimental plots were situated a minimum of 25 cm from the edge of each *A. californica* cluster and from other plots. The plots were 50 cm \times 50 cm, with treatments extending an additional 10 cm beyond the plot boundary. Plot locations were assigned randomly within eight replicate blocks, each of which was located within a single cluster of shrubs and included all four treatment combinations. Within blocks, plot orientations were assigned non-randomly to include a single shrub immediately outside the plot at one end and a gap in the shrub canopy (no shrub canopy directly overhead) at the other end. This plot orientation allowed investigation of the importance of gaps in the distribution of understory herbs beneath a CSS canopy. Each plot was divided into two 25 cm \times 50 cm subplots: one under the canopy and one in the adjacent gap.

Experimental Treatments

Seed addition. We amended plots with seed from five native annual forb and two annual legume species at a density of 4.5 g m⁻² per taxon (Table 1). All seeds were obtained commercially from S&S Seeds (Carpinteria, CA). Plots were seeded on 19 February 2004. Prior to seed addition, the soil was disturbed by hand-raking to a depth of 2 cm. Control plots were similarly disturbed. After seed addition, the loosened soil

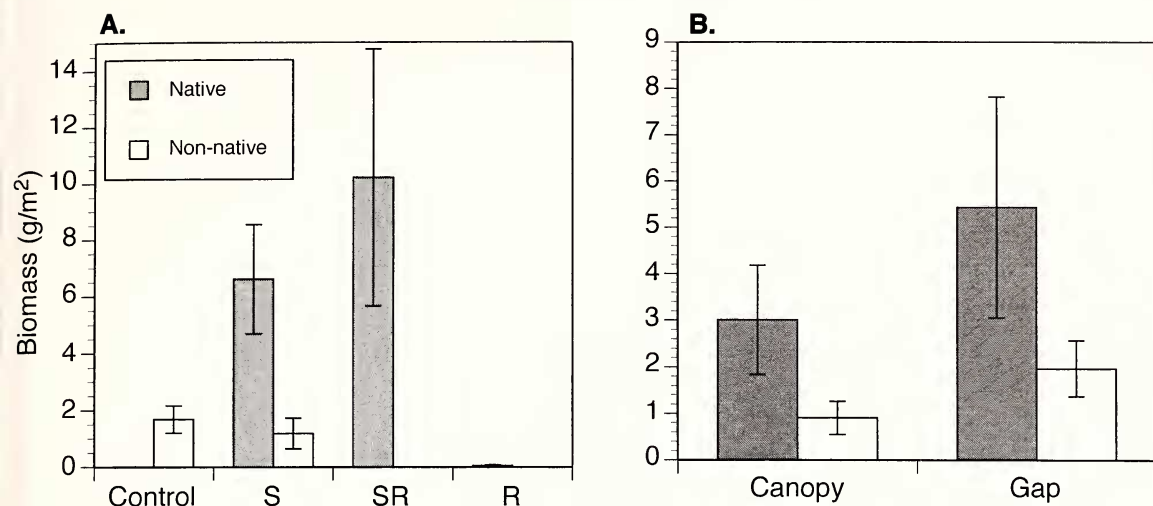


FIG. 1. Biomass of native (shaded bars) and non-native (open bars) species in (A): plots with native seed addition only (S), seed addition and non-native species removal (SR), non-native species removal only (R), and no treatment (control), and (B): subplots beneath the shrub canopy and in gaps. In control and R plots, *Artemisia californica* was the only native present. In S and SR plots, most of the native biomass was from *Lasthenia californica*. Bars are means \pm 1 SE.

was spread over the seeds to minimize losses from wind, runoff, and predation. Because rainfall was below average during the experiment, supplemental water was provided in late March and early April to prevent excessive mortality.

Seeded species were harvested on 12 May 2004, at the end of the growing season. To determine if seed addition had an effect on any preexisting native understory, all volunteer native species were collected as well. Aboveground biomass was dried for 48 hr at 60°C and weighed.

Non-native species removal. All non-native species were removed from weeded plots by clipping at ground level. Early germinating species were removed on 9 March, as soon as plants were identifiable. A second removal was performed on 1 April to remove later germinating species. No non-native species were observed in any weeded plots after the second removal. Non-natives from unweeded plots were harvested, dried, and weighed with native species at the end of the growing season.

Soil moisture and light availability. Photosynthetically active radiation (PAR) was measured in each subplot within 2 hr of solar noon on 29 April. Values were recorded as the ratio of light measured below the canopy to incident light measured directly above the canopy. Soil moisture in the top 12 cm of soil was also recorded using a Hydrosense TDR probe (Campbell Scientific, Logan, UT). Deeper readings were not taken to avoid excessive disturbance within the plots and because the rocky soil made probe insertion difficult. Three soil moisture readings were taken from each subplot, and the results

were averaged prior to analysis. Soil moisture was recorded on 11 May, one day prior to harvesting all aboveground biomass in the plots.

Statistical Procedures

To meet assumptions of normality and homogeneity of variance, a natural log transformation on all biomass measurements was performed, and soil moisture measurements were rank transformed. Because light intensity measurements were normally distributed, they were not transformed.

To determine how shrubs influenced light and soil moisture, a paired t-test was conducted to compare light intensity between canopy and gap subplots, and a Wilcoxon signed rank test was used to test for a soil moisture difference between subplot types.

We used analysis of covariance to examine effects of seed addition, non-native removal, light, and soil moisture on the biomass of native herbs. A similar analysis was used to test effects of native seed addition, light, and soil moisture on non-native biomass within non-removal plots.

RESULTS AND DISCUSSION

Native Seed Addition

Native seed addition significantly increased native understory biomass. Native biomass in seed addition plots averaged $8.41 \pm 2.45 \text{ g m}^{-2}$, compared to $0.03 \pm 0.02 \text{ g m}^{-2}$ in control plots ($F_{1,50} = 310$, $P < 0.001$; Fig. 1a). Natives averaged 2.6% of total herbaceous biomass in

unseeded, unweeded plots and 88.5% in seeded, unweeded plots.

Although all seven seeded species were observed germinating, only *Lasthenia californica* (Asteraceae) and *Amsinkia menziesii* (Boraginaceae) survived long enough to produce flowers (Table 1). *Lasthenia californica* produced 98% of native biomass, while *A. menziesii* produced the remaining 2%. The only volunteer natives observed were *A. californica* seedlings.

No substantial populations of native CSS herbs were observed within several hundred meters of the study site, and it is likely that seed dispersal beyond this distance is very low (Van Dorp et al. 1996; Jongejans and Schippers 1999). Furthermore, the absence of any native herbaceous growth in unseeded plots suggests that no native seed bank remained on the site. Past disturbance and several decades of non-native species dominance has likely eliminated any native seed bank that may have been present. Because an impoverished native seed bank and few local seed sources may be typical of many potential CSS restoration sites, seed addition of understory herbaceous plants is likely to be a necessary component of many restoration projects.

Competition

In unweeded plots, native seed addition caused a small but significant decline in non-native biomass, from 1.68 g m^{-2} to 1.19 g m^{-2} ($F_{1,20} = 4.76$, $P = 0.04$; Fig 1a). The small magnitude of this change is likely due to low non-native biomass throughout the planted area. The high biomass of *L. californica* in seeded plots suggests that this species, if seeded at high densities, may be effective at controlling non-native species.

There were no significant effects of non-native removal on native biomass, regardless of seeding treatment. However, due to low non-native biomass and low survival of most seeded native species, it is difficult to make any conclusions about a competitive effect of non-native species on natives. Strong competitive effects of non-native species in CSS and similar systems have been demonstrated in the past, and may have been observed in this system had non-natives been more abundant (D'Antonio and Vitousek 1992; Eliason and Allen 1997; but see Seabloom et al. 2003b).

Shrub Effects

As expected, light intensity was significantly lower beneath the canopy (mean $47 \pm 3.0\%$) than it was in gaps ($74 \pm 3.0\%$). There was no significant difference in soil moisture between canopy and gap subplots. Native understory biomass did not differ significantly between the

shrub canopied and gap plots, suggesting that any competitive effect of shrubs on the natives may have been balanced by a facilitative effect. Non-native biomass was significantly less beneath the canopy ($F_{1,20} = 5.80$, $P = 0.03$; Fig. 1b). This was likely due to the large reduction in light intensity beneath the canopy, although it may also be due to belowground effects not measured in this study.

Soil Moisture

There was a significant positive relationship between soil moisture and native biomass ($F_{1,50} = 5.54$, $P = 0.02$), but not between soil moisture and non-native biomass. Although soil moisture was limiting for both natives, the importance of soil moisture may have been exaggerated by the very low precipitation throughout the growing season. Low soil moisture may also explain the high mortality observed for most seeded native species. These species were observed germinating, but died during mid-season when rainfall also declined sharply below weekly averages. Finally, the lack of a difference in native growth between low light (canopied) and high light (gap) subplots would be expected if soil moisture was more limiting than light, and shading by shrubs reduced water stress for the native understory.

Conclusions

This study suggests that in restored dense-canopy CSS, soil moisture is an important limiting factor for native understory species, while light is more limiting for non-natives. Non-natives were also more abundant in gaps than they were beneath the shrub canopy, suggesting a competitive effect of the shrubs. Thus, the presence of a mature, dense shrub layer may effectively exclude a large fraction of non-native species without adversely affecting some native species.

Competition with the restored native understory (which consisted primarily of *L. californica*) significantly reduced non-native biomass. Thus, the addition of seeded native understory herbs may be an effective secondary restoration strategy, particularly given that long distance dispersal of native understory herbs is likely to be a rare event. Seeding may be accomplished at a fairly low cost and can successfully establish some native herbs and reduce the abundance of non-native species.

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LITERATURE CITED

- BOWLER, P. A. 2000. Ecological restoration of coastal sage scrub and its potential role in habitat conservation plans. *Environmental Management* 26:S85–S96.
- D'ANTONIO, C. M. AND P. M. VITOUSEK. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* 23:63–87.
- DAVIS, F. W., P. A. STINE, AND D. M. STOMS. 1994. Distribution and conservation status of coastal sage scrub in southwestern California. *Journal of Vegetation Science* 5:743–756.
- DYER, A. D. AND K. J. RICE. 1999. Effects of competition on resource availability and growth of a California bunchgrass. *Ecology* 80:2697–2710.
- ELIASON, S. A. AND E. B. ALLEN. 1997. Exotic grass competition in suppressing native shrubland reestablishment. *Restoration Ecology* 5:245–255.
- FREUDENBERGER, D. O., B. E. FISH, AND J. E. KEELEY. 1987. Distribution and stability of grasslands in the Los Angeles basin. *Bulletin of the Southern California Academy of Sciences* 86:13–26.
- HICKMAN, J. C. (ed.). 1993. *The Jepson manual: higher plants of California*. University of California Press, Berkeley, CA.
- HUMPHREY, L. D. AND E. W. SCHUPP. 2004. Competition as a barrier to establishment of a native perennial grass (*Elymus elymoides*) in alien annual grass (*Bromus tectorum*) communities. *Journal of Arid Environments* 58:405–422.
- JONGEJANS, E. AND P. SCHIPPERS. 1999. Modeling seed dispersal by wind in herbaceous species. *Oikos* 87:362–372.
- MELGOZA, G., R. S. NOWAK, AND R. J. TAUSCH. 1990. Soil water exploitation after fire: competition between *Bromus tectorum* (cheatgrass) and two native species. *Oecologia* 83:7–13.
- MINNICH, R. A. AND R. J. DEZZANI. 1998. Historical decline of coastal sage scrub in the Riverside-Perris plain, California. *Western Birds* 29:366–391.
- O'LEARY, J. F. 1995. Coastal sage scrub: threats and current status. *Fremontia* 23(4): 27–31.
- AND W. E. WESTMAN. 1988. Regional disturbance and effects on herb succession patterns in coastal sage scrub. *Journal of Biogeography* 15:775–786.
- SEABLOOM, E. W., W. S. HARPOLE, O. J. REICHMAN, AND D. TILMAN. 2003a. Invasion, competitive dominance, and resource use by exotic and native California grassland species. *Proceedings of the National Academy of Sciences* 100:13384–13389.
- , E. T. BORER, V. L. BOUCHER, R. S. BURTON, K. L. COTTINGHAM, L. GOLDWASSER, W. K. GRAM, B. E. KENDALL, AND F. MICHELI. 2003b. Competition, seed limitation, disturbance, and reestablishment of California native annual forbs. *Ecological Applications* 13:575–592.
- THOMPSON, L. AND J. HARPER. 1988. The effect of grasses on the quality of transmitted radiation and its influence on the growth of white clover *Trifolium repens*. *Oecologia* 75:343–347.
- VAN DORP, D., W. P. M. VAN DEN HOEK, AND C. DALEBOUDT. 1996. Seed dispersal capacity of six perennial grassland species measured in a wind tunnel at varying wind speed and height. *Canadian Journal of Botany* 74:1956–1963.
- WESTMAN, W. E. 1981. Diversity relations and succession in Californian coastal sage scrub. *Ecology* 62:170–184.